Expanded dorsal ribs in the Late Triassic pseudosuchian reptile Euscolosuchus olseni

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Abstract: The presence of expanded dorsal ribs is an unusual feature found only in a small number of tetrapod taxa. This condition, characterized by broadening of much of the entire rib shaft, differs from one where only a portion of the rib shaft is expanded or bears an uncinate process (e.g., birds, crocodylians, and Sphenodon; Jenkins, 1970). Recently, there has been renewed interest in the structure and development of dorsal ribs among amniotes in connection with the evolutionary development of the carapace in turtles (Lyson et al., 2013; Schoch and Sues, 2015). Reinterpretation of the anteroposteriorly broadened dorsal ribs in the Middle Permian putative stem turtle Eunotosaurus (Lyson et al., 2013) and the discovery of similar ribs in the more derived Triassic stem turtles Odontochelys (Li et al., 2008) and Pappochelys (Schoch and Sues, 2015) suggest that this feature represented an important step in the early evolution of the turtle carapace. Sues (1992) described a series of dissociated cervical and dorsal osteoderms and an incomplete dorsal vertebra of a new archosaurian reptile, Euscolosuchus olseni, from the Vinita Formation (formerly Turkey Branch Formation; Upper Triassic: Carnian) in the Richmond Basin of the Newark Supergroup at Midlothian, Virginia. Sues et al. (1994) have discussed the fossil locality and its geological context. Based on apomorphic features of the osteoderms, which formed two rows of dermal armor over at least the neck and trunk, Sues (1992) suggested referral of Euscolosuchus olseni to Pseudosuchia (Crurotarsi). A nearly complete rib was found together with disarticulated but still associated osteoderms and a dorsal vertebra of Euscolosuchus olseni. It was not included in the original description by Sues (1992) because it was not recognized as a rib at the time. In addition, a proximal end of another rib was recovered on an earlier occasion, but it articulates almost perfectly with the left transverse process of the dorsal vertebra. Referral of these elements to Euscolosuchus olseni is further supported by the distinctive external ornamentation on part of the rib shaft, which is indistinguishable from that on the external surfaces of the osteoderms and comprises round to oval pits of various sizes bounded by low ridges. The ribs clearly differ in their structure from those of Doswellia kaltenbachi, an unusual, heavily armored non-archosaurian archosauriform recovered from the Falling Creek Formation (Carnian) of Hanover County, Virginia (Dilkes and Sues, 2009). We here present a description of the two rib fragments referred to Euscolosuchus olseni and review their possible.

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SHORT COMMUNICATION

EXPANDED DORSAL RIBS IN THE LATE TRIASSIC PSEUDOSUCHIAN REPTILE *EUSCOLOSUCHUS OLSENI*

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The presence of expanded dorsal ribs is an unusual feature found only in a small number of tetrapod taxa. This condition, characterized by broadening of much of the entire rib shaft, differs from one where only a portion of the rib shaft is expanded or bears an uncinate process (e.g., birds, crocodylians, and *Sphenodon*; Jenkins, 1970). Recently, there has been renewed interest in the structure and development of dorsal ribs among amniotes in connection with the evolutionary development of the carapace in turtles (Lyson et al., 2013; Schoch and Sues, 2015). Reinterpretation of the anteroposteriorly broadened dorsal ribs in the Middle Permian putative stem turtle *Eunotosaurus* (Lyson et al., 2013) and the discovery of similar ribs in the more derived Triassic stem turtles *Odontochelys* (Li et al., 2008) and *Pappochelys* (Schoch and Sues, 2015) suggest that this feature represented an important step in the early evolution of the turtle carapace.

Sues (1992) described a series of dissociated cervical and dorsal osteoderms and an incomplete dorsal vertebra of a new archosaurian reptile, *Euscolosuchus olseni*, from the Vinita Formation (formerly Turkey Branch Formation; Upper Triassic: Carnian) in the Richmond Basin of the Newark Supergroup at Midlothian, Virginia. Sues et al. (1994) have discussed the fossil locality and its geological context. Based on apomorphic features of the osteoderms, which formed two rows of dermal armor over at least the neck and trunk, Sues (1992) suggested referral of *Euscolosuchus olseni* to Pseudosuchia (Crurotarsi). A nearly complete rib was found together with disarticulated but still associated osteoderms and a dorsal vertebra of *Euscolosuchus olseni*. It was not included in the original description by Sues (1992) because it was not recognized as a rib at the time. In addition, a proximal end of another rib was recovered on an earlier occasion, but it articulates almost perfectly with the left transverse process of the dorsal vertebra. Referral of these elements to *Euscolosuchus olseni* is further supported by the distinctive external ornamentation on part of the rib shaft, which is indistinguishable from that on the external surfaces of the osteoderms and comprises round to oval pits of various sizes bounded by low ridges. The ribs clearly differ in their structure from those of *Doswellia kaltenbachi*, an unusual, heavily armored non-archosaurian archosauriform recovered from the Falling Creek Formation (Carnian) of Hanover County, Virginia (Dilkes and Sues, 2009). We here present a description of the two rib fragments referred to *Euscolosuchus olseni* and review their possible implications.

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Institutional Abbreviation—USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C.

METHODS

The better-preserved specimen, USNM 544104, was sectioned longitudinally and transversely to assess its histological structure, both in the proximal part as well as in the more distally situated ornamented shaft region. After molding and prior to sectioning with a diamond-sintered saw blade, the specimen was embedded in Technovit synthetic resin to prevent spalling of the outermost bony lamellae. Using the petrographic sectioning procedure outlined by Scheyer et al. (2014), sections were then ground manually using a series of silicon carbide powders (SiC 500, 800) to a thickness of 60 to 80 μm. The thin-sections were studied using a Leica compound microscope DM 2500 M equipped with a Leica digital camera DFC 420C.

DESCRIPTION

USNM 448590

This specimen is an incomplete right rib that lacks part of the bony substance of the anteroposteriorly broad and ornamented shaft (Fig. 1). Fortunately, distinct impressions in the matrix on both the part and counterpart blocks of this specimen permit reconstruction of the rib.

Details of the impression of the proximal rib head are difficult to interpret. The somewhat constricted 'neck' region is more strongly flattened dorsoventrally than in USNM 554104 and has an almost flat rather than concave, smooth dorsal surface. It is 16 mm wide at the widest point and up to 6 mm thick at the broken proximal end. Its anterior margin is more rounded and thicker than its posterior edge. The ventrolaterally and posteromedially extending expanded portion of the rib shaft is set off from the 'neck' portion by an angle of about 45°. Its greatest width is 35.05 mm, and it is about 80 mm proximodistally. The expanded region has a nearly straight posterior and a convex anterior edge and tapers slowly toward the apparently rounded-off distal end, resulting in a leaf-like outline. Its external surface is gently convex dorsoventrally and anteroposteriorly. The posterior portion of the expanded portion of the rib extends much further posteriorly relative to the neck region than the anterior one does anteriorly. Except for an about 6-mm-wide band along the anterior margin of the rib, the lateral surface of the proximal region of the expansion bears well-developed ornamentation comprising pits with greatest diameters ranging from 2 to 3 mm and bounded by low ridges. This

FIGURE 1. Right dorsal rib of *Euscolosuchus olseni*, USNM 448590, in external view (**A**) and with outlines superimposed on photograph (**B**). Both scale bars equal 1 cm.

ornamentation becomes gradually less pronounced distally and, about 40 mm from the proximal terminus of the ornamented surface, grades into more confluent pits and then, more distally, into slight, irregular vertical grooving (Fig. 1B). The band along the anterior margin of the rib expansion lacks pits but bears striations, which possibly represent points of attachment for intercostal muscles. The medial (visceral) surface of the expanded portion of the rib is smooth and featureless.

USNM 544104

This specimen represents the proximal portion of a left dorsal rib (Fig. 2A, B). It comprises the proximal articular end (rib

FIGURE 2. *Euscolosuchus olseni*, proximal portion of a left dorsal rib, USNM 544104. **A**, view of the proximal articular surface; **B**, external view of the rib fragment. The specimen was first sectioned proximally (longitudinally) and the remaining part transversely. The arrows in **B** mark the position of the sections shown in Figure 3A and B. **Abbreviations**: **ca**, capitulum; **fo**, fossa; **tu**, tuberculum. Scale bar equals 1 cm.

head), an unsculptured, slightly constricted 'neck' region, and a segment of the expanded rib shaft with a small (14 × 17 mm) patch of external ornamentation on its lateral surface. The ornamentation consists of round to oval pits of various sizes bounded by low ridges, similar to that on the external surfaces of the osteoderms of *Euscolosuchus olseni*. The ornamented portion of the rib extends ventrolaterally at an angle of about 45° to the more proximal portion and expands posteriorly. The thickness of the rib in longitudinal section is greatest at the preserved posterior end of the ornamented patch. The largest pit is about 3 mm in greatest diameter and between 1 and 1.2 mm deep in relation to the surrounding ornamental ridges. Both cortices are fairly constant in thickness throughout the section, with the thickness of the external one ranging from 0.85 to 1.15 mm and that of the internal one from 0.8 to 1.25 mm. The thickness of the interior cancellous bone ranges from 1.5 to 3.5 mm (the latter again being present in the bent region).

The 'neck' region of the rib is 16 mm wide at its widest point and 4.5 mm thick in cross-section (Fig. 3A). Its dorsal surface is concave and the ventral surface convex. The anterior margin is rounded and the posterior one forms a marginal ridge that tapers distally. At the tapering margin, the cortical bone is 0.3 to 0.75 mm thick, whereas its thickness ranges from 0.6 to 1.1 mm along the rounded margin. The shape and extent of the internal cancellous bone essentially mirrors that of the external bone surface.

The cortical bone is structurally identical in the expanded ornamented portion and the smooth-surfaced part of the 'neck' region near the proximal end (Fig. 3B, C). It comprises a parallel-fibered to lamellar bone matrix deposited by cyclical growth, in which the bone-cell lacunae have oblong flattened shapes. The ridges surrounding the ornamental pits grow in height by specific bone deposition and, to a lesser degree, by resorption, with the pits increasing in size through ontogeny.

Vascularization of the compact bone tissue is generally low, consisting of sparsely scattered simple primary vascular canals. In cross-section, these canals are visible as small round to oval spaces, but, in longitudinal section, it is apparent that the canals do not simply extend longitudinally through the rib but extend at high angles from the cancellous interior to the external rib surface. Eight or nine growth cycles could be identified in the compacta represented by growth zones followed by thin annuli and lines of arrested growth. These are most distinct in the dorsal cortex (Fig. 3D). The remodeling processes and expansion of the interior cancellous bone have certainly erased some of the earlier growth record, but given the irregular thickness of growth zones and diagenetic alteration of the interior bone tissue, we refrain from retro-calculating and counting these earlier cycles. The specimen possibly had already attained skeletal maturity because the last four growth zones are definitely closely spaced in the outermost compacta. There is, on the other hand, no indication of the onset of sexual maturity in the growth record (such as a change in tissue type, vascularization, or cycle thickness apart from the last four growth zones mentioned above). In the cross-section of the rib shaft, coarse Sharpey's fibers are visible extending into the cortical bone at high angles on both rib margins. In accordance with previous studies (e.g., Jenkins, 1970; Lyson et al., 2013; Waskow and Sander, 2014), these features are interpreted as attachment sites for intercostal muscles.

The cancellous interior of the rib is a remodeled trabecular network, in which the trabeculae consist of endosteally deposited secondary lamellar bone (Fig. 3C). Internally, the trabeculae have been broken due to postmortem compaction, with bone debris now filling in some of the vascular cavities. Scattered larger erosion cavities are also found in the cortex remodeling the compact bone, but with the exception of the largest and deepest ornamental pits, the cavities do not reach the external bone surface.

The proximal articular end of USNM 544104 (greatest width: 22.7 mm) has a structure unlike that in any other known archosauriform (Fig. 2). In addition to the capitular and tubercular facets, there is a deep recess immediately posterior to the capitular facet. This recess is separated from the tubercular facet behind it

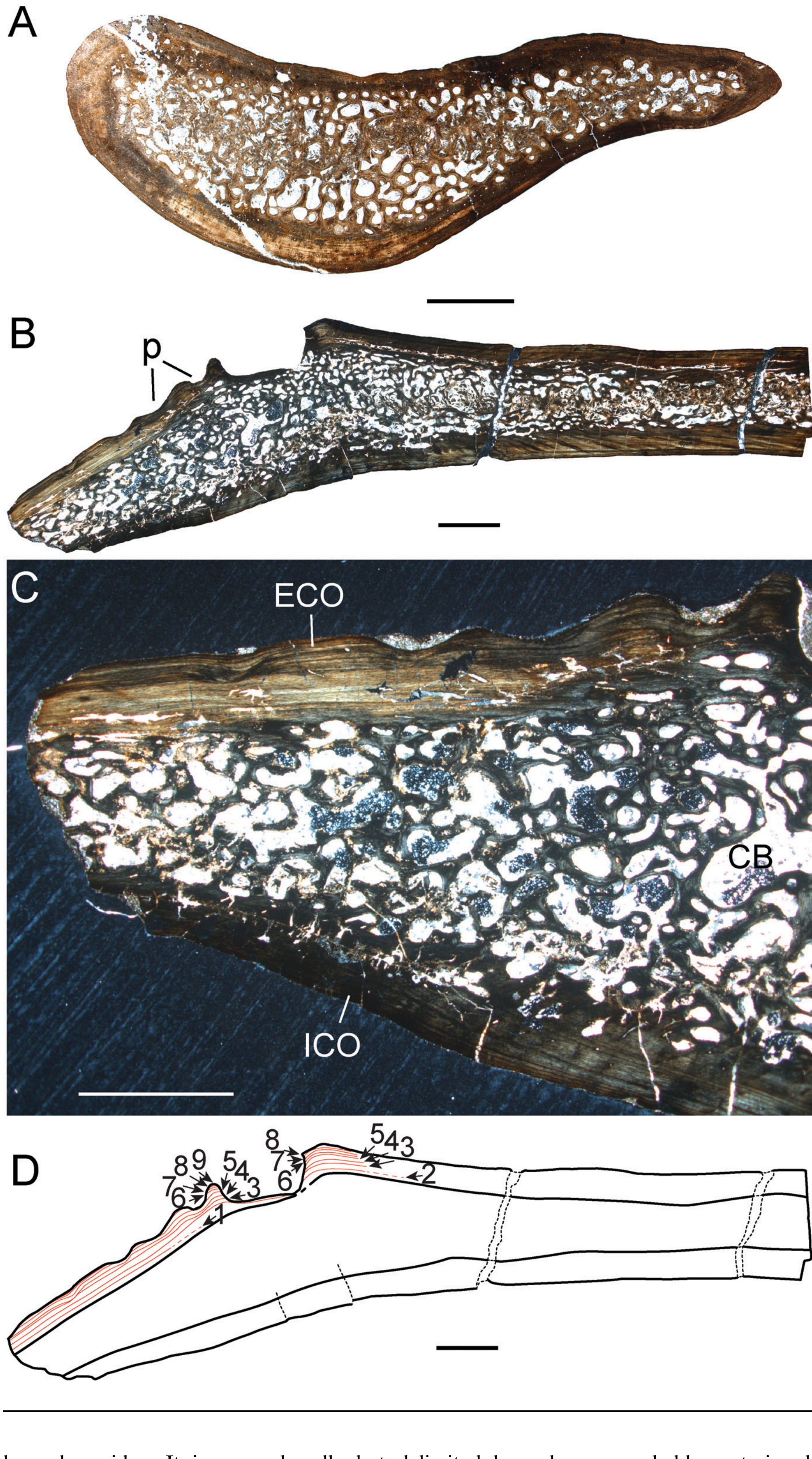

FIGURE 3. *Euscolosuchus olseni*, proximal portion of a left dorsal rib, USNM 544104. **A**, transverse section through the 'neck' region of the fragment. **B**–**D**, longitudinal section, with growth lines (highlighted in red) in the dorsal cortical bone shown in **D**. **C**, close-up of the ornamented lateral portion of the rib. Note the absence of relief of the growth marks in the deepest compact layers, whereas the relief increases towards the external surface of the bone. **D**, schematic interpretation of growth lines within the external cortex. On the most prominent (proximal) ornamental ridges, a maximum of eight or nine growth lines is visible (marked by black arrows and numbers). **Abbreviations**: **CB**, cancellous bone; **ECO**, external cortex; **ICO**, internal cortex; **p**, pit. Scale bars each equal 2 mm.

by a low ridge. It is open dorsally but delimited by a bony 'lip' ventrally. The tubercular facet (greatest length: ca. 7 mm) is positioned further laterally than the capitular one and is narrower dorsoventrally than the latter (greatest length: ca. 8 mm). The structure of the articular end of the rib head closely matches that of the distal articular area on the left transverse process of a probable posterior dorsal vertebra (USNM 448584) reported by Sues (1992). The identification of the rib necessitates reinterpretation of articular features at the distal end of that process. The anterior of three rib facets originally identified (Sues, 1992:fig. 2C) is the damaged area for the capitular facet of the rib head, but the other two 'facets' are concavities flanking a robust vertical ridge between the areas for the capitular and tubercular facets of the rib head. This vertical ridge would fit into the depression between the capitular and tubercular facets on the rib head. Triple-headed ribs have been reported in some archosauriform reptiles (e.g., *Erythrosuchus*; Gower, 2003), but in these taxa, each articular facet on the rib head has its own peduncle.

DISCUSSION

External ornamentation on ribs is highly unusual among tetrapods. In addition to the example reported here, we only know of ornamented (and expanded) trunk ribs in an as yet undescribed skeleton of the murid rodent *Afrocricetodon songhori* from the Miocene of Kenya (Shipman, 1981:fig. 6.2). In *Euscolosuchus olseni*, one could have expected fusion of an ornamented dermal ossification directly onto an otherwise smooth-surfaced endoskeletal rib. However, the histological data presented above are inconsistent with this interpretation. There is no evidence for co-ossification of a superficial osteoderm with the underlying rib nor are there any unconformities or relics of primary bone matrix in the cancellous bone that would hint at co-ossification at earlier ontogenetic stages. Instead, we see that the deepest layers within the external primary cortex had only very weak ornamental relief or that the bone surface was smooth and that the ornamental relief became more pronounced with additional growth of the rib.

The processes leading to the pattern of pits bounded by bony ridges on the ribs of *Euscolosuchus olseni* (Figs. 1, 2B) resemble those described for cranial bones and osteoderms of crocodylians (Buffrénil et al., 2015). In both cases, the pits are stationary and increase in size throughout ontogeny by interplay of bone deposition and resorption processes. In *Euscolosuchus olseni*, however, there is no indication of drifting pits or of extensive deposition and remodeling cycles that would leave behind a stack of cementing lines within the pits, as described by Buffrénil et al. (2015) for crocodylian bones. Instead, the ridges (and thus the pits) on the rib of *Euscolosuchus olseni* increase in height and diameter mostly by preferential deposition of bone augmenting the relief of the bone surface. This pattern is also present elsewhere among temnospondyls (Witzmann and Soler-Gijón, 2010) and turtles (Scheyer et al., 2012). The ornamentation on the more proximal portion of the ribs suggests dermal influence during ossification. Recently, Clarac et al. (2015) quantified the area gain due to ornamentation on crocodylian cranial bones and osteoderms. Considering competing functional hypotheses for such increased bone ornamentation (including gas exchange, anchoring of skin, mechanical reinforcement, and thermal exchange), the authors indicated that the thermal exchange between body and environment might play an especially important role, at least in crocodylians. The lesser degree of remodeling and the preferential mode of bone deposition at the ridges allowing for an increased anchoring of overlying dermal tissue may indicate that a heat exchange function for the ornamented bones of *Euscolosuchus* might have been less important than for extant crocodylians.

The function of expanded ribs has been extensively discussed, but few conclusions have been reached (Jenkins, 1970). In the case of *Euscolosuchus olseni*, one plausible explanation is increased rigidity of the trunk region. This would be consistent with the interlocking mode of articulation between the cervical and dorsal osteoderms, which would have largely suppressed lateral flexion in the neck and trunk regions (Sues, 1992). It is also possible that the osteoderms and ribs restricted movement of the trunk to reduce torsional or shear stresses on the vertebral column. Based on the structure of the single dorsal vertebra, which has a low neural spine, and the overlying osteoderms with long anterolateral processes, there was little room for epaxial musculature. Unfortunately, too little is still known about the structure of the skeleton of this unusual pseudosuchian to explore the possible functional significance of the postcranial axial skeleton in more detail.

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